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FACTORS AFFECTING CURLY-TOP INFECTIVITY OF BEET LEAFHOPPER, EUTETTIX TENELLUS[1]

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INTRODUCTION

A NUMBER OF INVESTIGATORS have called attention to the fact that large numbers of beet leafhoppers, *Eutettix tenellus* (Baker), collected in the foothill breeding areas and on weeds in the cultivated areas, failed to transmit the curly-top virus to sugar beets. There have been occasional reports in the literature of large populations of leafhoppers in beet fields with a small amount of curly top developing during the season.

Smith and Boncquet (*23*)[3] tested fully 2,000 beet leafhoppers taken on *Atriplex tularensis* and *Chenopodium album* in the Tulare Lake region of the San Joaquin Valley upon several hundred sugar-beet plants without the production of curly top in a single instance.

Boncquet and Hartung (*1*) report that 100 leafhoppers collected on species of *Artemisia* and *Atriplex* in the Tulare Lake region and confined singly in cages on beet seedlings failed to produce curly top. Hartung (*5*), in a detailed paper on the results of the same experiment, states that 87 insects were tested and that 7 per cent "probable" cases of curly top developed. These "probable" cases of curly top showed one or more slightly curled leaves, but no reliable symptoms of the disease, such as wartlike protuberances on the lower surface of the leaves.

Hartung (*6*) tested 2 lots of leafhoppers collected on the foothills, and

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[3] Italic numbers in parenthesis refer to "Literature Cited" at the end of this paper.

found that 6 per cent of one and 30 per cent of the other transmitted the curly-top virus to sugar beets.

Hartung (*5*) found the beet leafhopper abundant in a field of beets just being thinned at Visalia on April 20, 1915, and when he again visited the beet field on June 5, only slight indications of curly top were present. He concluded that a high percentage were unable to transmit the curly-top virus.

A number of lines of investigation were followed in an attempt to determine the percentage of leafhoppers infective in different localities in the state and in different years, and to analyze the factors that may be involved. To this end, tests were made to determine whether leafhoppers collected many miles from sugar-beet fields are infective; what percentage of leafhoppers are infective on the foothills of the San Joaquin and Salinas valleys and in the cultivated areas; whether food plants immune to curly top affect the period of infectivity of the insect; what percentage of infectivity is shown by insects reared on weeds that attenuate the curly-top virus; whether the virus can be recovered from infected perennials repeatedly and at different seasons, and from infected annuals repeatedly during the life of the plants. Some further tests were also conducted on the host range and reservoirs of curly top on the uncultivated plains and foothills, and on the recovery of the virus from the most important breeding plants by single insects.

METHODS

In collecting beet leafhoppers under natural conditions, general sweepings were made on pasture vegetation, preferably on one species of plant, although this was not always possible. The leafhoppers taken on each species of plant were removed from the insect net with a pipette described in a previous paper (*15*) and transferred to a cage. On red-stem filaree (*Erodium cicutarium*) growing on the foothills, nymphs were usually captured with a pipette. In beet fields the overwintering females were disturbed by moving the hand among the leaves, and then the insects were caught with a pipette. The vegetation on which leafhoppers were captured was not used as food because there was a possibility that some of the plants were infected with curly top, and hence the insects while in the field were fed in cages on the foliage of Mammoth or Alameda sweet corn (*Zea Mays*), which is immune to curly top.

In determining the percentage of infective beet leafhoppers under natural conditions, from 25 to 100 nymphs or adults were collected on the foothills or in the cultivated areas, and then each specimen was confined in a cage enclosing a healthy sugar-beet seedling in the greenhouse.

During the years 1926 to 1933 but not during 1924, each leafhopper was fed on the first beet for a period of 2 weeks and then was provided with a second healthy beet, except those specimens which had transmitted the curly-top virus to the first plant.

INFECTIVITY OF BEET LEAFHOPPERS IN DESERT, FOOTHILL, AND CULTIVATED AREAS

Near and Away from Beet Fields.—In 1918, tests were made to determine whether beet leafhoppers were infective in localities where no sugar beets were grown and also in the vicinity of beet fields. The results are given in table 1. Adults were collected on different species of plants

TABLE 1

PLANTS FROM WHICH BEET LEAFHOPPERS TRANSMITTED CURLY-TOP VIRUS TO SUGAR BEETS

District	Plants on which insects were collected: Common name	Plants on which insects were collected: Scientific name	Number of insects tested	Date insects were collected, 1918
Imperial Valley, away from beet fields:				
Dixieland	Lowland purslane	*Sesuvium sessile*	7 adults	Mar. 13
Calexico	Lowland purslane	*Sesuvium sessile*	300 adults	Apr. 2
Niland	Wheelscale	*Atriplex elegans*	25 nymphs	Apr. 21
			200 adults	Apr. 21
Mojave Desert, 2 to 4 miles from beet fields near Victorville	Creosote bush	*Larrea tridentata* var. *glutinosa*	14 adults	Jan. 30
Salinas Valley:				
King City, near beet fields	Red-stem filaree	*Erodium cicutarium*	3 adults	May 27
King City, foothills	Red-stem filaree	*Erodium cicutarium*	3 nymphs	Nov. 28
Bitterwater, foothills	Red-stem filaree	*Erodium cicutarium*	100 adults	Oct. 13
San Joaquin Valley:				
Foothills 13 miles southwest of Tracy	Red-stem filaree	*Erodium cicutarium*	12 adults	Dec. 10
			18 nymphs	Dec. 24
			25 adults	Dec. 24

growing in the Imperial Valley, where no sugar beets were grown during 1918, and each lot, varying in number from 7 to 300 specimens, transmitted the curly-top virus to sugar beets. In the Mojave Desert, leafhoppers collected on creosote bush (*Larrea tridentata* var. *glutinosa*), from 2 to 4 miles away from beet fields near Victorville, were found to be infective; the adults were collected on January 30 after the beets had been harvested. Nymphs and adults collected on the foothills of the Salinas and San Joaquin valleys transmitted the curly-top virus to sugar beets. Beets were grown near King City in the Salinas Valley and near

Tracy in the San Joaquin Valley, but not near Bitterwater, situated in a mountain pass in the Gabilan Mountains.

In Little and Big Panoche Passes.—During 1924, the adults of the spring generation were captured in many localities on the foothills and floor of Little Panoche Pass, situated in the middle San Joaquin Valley. In the greenhouse, 50 males and 50 females were confined singly in 100 cages, each enclosing a healthy beet seedling, and every insect that had not transmitted the virus was transferred every two weeks to a healthy beet seedling for a period of 16 weeks. The experiment was begun on April 10 and ended on August 1.

Nine males and 8 females, or 17 per cent (table 2), transmitted the curly-top virus to sugar beets. Eight males and 7 females infected the first beet. One insect infected the second beet but not the first; another infected the third but not the first two: in other words, periods of at least 14 and 28 days, respectively, elapsed before infections occurred.

In a previous paper (*11*), it was reported that when infective males that had completed the nymphal stages on diseased beets, were provided with a healthy beet daily during adult life, there were periods of from 8 to 56 days in which no infections occurred. The 14- and 28-day periods mentioned in the preceding paragraph may correspond to intervals between infections or may represent long incubation periods of the virus in the beet leafhoppers which had fed for short periods on diseased beets as reported by Freitag (*4*).

During 1926 the percentage of females infective in the overwintering generation was compared with that of the adults infective in the spring generation. In one test, the overwintering females and the adults of the spring generation were collected on *Erodium cicutarium* in many favorable localities in Little Panoche Pass, and in another test the adults of both generations were taken abundantly in the corresponding localities on a foothill near the entrance of Big Panoche Pass. The results are given in table 2. The percentage of infectivity is higher with adults of the spring generation than with the overwintering females. The overwintering adults, however, were collected on March 2, and it has been demonstrated that leafhoppers near the end of their natural life do not produce curly top so often as during early adult life (*4, 11*). The overwintering females die during March and early April on the uncultivated plains and foothills (*15*).

During 1929, 1930, and 1931, only adults of the spring generation were collected and tested, and only in Little Panoche Pass. The results are shown in table 2.

During 1932, the percentages of females infective in the overwinter-

TABLE 2

PERCENTAGE OF INFECTIVE BEET LEAFHOPPERS UNDER NATURAL CONDITIONS

Year and locality	Food plant	Date	Generation	Number	Per cent of infective insects
Uncultivated plains and foothills, San Joaquin Valley					
1924					
Little Panoche Pass......	Pasture vegetation	Apr. 8	Spring	100	17
1926					
Little Panoche Pass......	*Erodium cicutarium*	Mar. 2	Overwintering	100	24
		Apr. 12	Spring	100	36
Big Panoche Pass........	*Erodium cicutarium*	Mar. 2	Overwintering	100	22
		Apr. 13	Spring	100	56
1929					
Little Panoche Pass......	Pasture vegetation	Apr. 10	Spring	100	16
1930					
Little Panoche Pass......	*Erodium cicutarium*	Apr. 3	Spring	100	2
1931					
Little Panoche Pass......	*Frankenia grandifolia*	Apr. 8	Spring	100	6
1932					
Little Panoche Pass......	*Erodium cicutarium*	Mar. 4	Overwintering	100	25
		Mar. 24	Spring	100	31
		Apr. 6	Spring	100	42
Hospital Canyon.........	*Erodium cicutarium*	Mar. 30	Spring	50	66
1933					
Little Panoche Pass......	*Frankenia grandifolia*	Apr. 10	Spring	100	16
Little Panoche Pass......	*Erodium cicutarium*	Apr. 11	Spring	100	37
Hospital Canyon.........	*Erodium cicutarium*	Apr. 18	Spring	100	53
Corral Hollow............	*Erodium cicutarium*	Apr. 18	Spring	100	46
Lone Tree Canyon.......	Pasture vegetation	Apr. 20	Spring	100	15
				100	12
Uncultivated foothills, Salinas Valley					
1926					
Foothills near San Ardo..	*Erodium cicutarium*	Feb. 23	Overwintering	100	65
		Mar. 21	Spring, nymphs	50	100
		Apr. 20	Spring, nymphs	50	100
		Apr. 20	Spring, adults	100	88
1932					
Pine Valley...............	*Erodium cicutarium*	Mar. 8	Overwintering	100	22
		Apr. 15	Spring	100	17
1933					
Hog Canyon.............	*Erodium cicutarium*	Apr. 13	Spring	100	16
Foothills near Metz.......	*Erodium cicutarium*	Apr. 13	Spring	100	9
Cultivated areas, Salinas Valley					
1926					
Gonzales to King City....	Sugar beets...........	Feb. 24	Overwintering	100	42
King City................	Weeds.................	Apr. 20	Spring	100	36
1932					
King City................	Sugar beets...........	Mar. 6	Overwintering	25	40
Metz.....................	Sugar beets...........	Mar. 8	Overwintering	100	11
King City................	Sugar beets...........	Apr. 15	Spring	25	12
Cultivated areas, San Juan Valley					
1932					
San Juan Valley..........	Sugar beets...........	Mar. 6	Overwintering	100	43

ing generation was again compared with that of adults infective in the spring generation collected in many localities on different dates in Little Panoche Pass. The infectivity tests are reported in table 2. Here again, a higher percentage of infectivity was obtained with the adults of the spring generation than with the overwintering females. The infectivity of the adults of the spring generation increased from 31 per cent on March 4, to 42 per cent on April 6.

During 1933, adults of the spring generation were collected on two species of food plants in Little Panoche Pass, and tests (table 2) showed more than twice as high a percentage infective on *Erodium cicutarium* as on *Frankenia grandifolia*. *F. grandifolia* is immune to curly top, and leafhoppers would not obtain the virus by feeding on this perennial plant, but, as shown later (p. 514), the period of infectivity in the leafhoppers is probably not affected by the juices from this plant. The period of infectivity of the leafhopper is not shortened by feeding infective adults on Mammoth or Alameda sweet corn (*Zea Mays*), also immune to curly top, and on Australian saltbush, or fleshscale (*Atriplex semibaccata*), which is highly resistant or immune to the disease as discussed later (p. 511).

In Canyons of the Northern San Joaquin Valley.—It has been assumed that higher percentages of infective leafhoppers occur in the northern canyons than in Little and Big Panoche passes of the San Joaquin Valley, owing to the fact that many overwintering adults reared on curly-top beets fly into the northern canyons and spread the virus to susceptible plants. The highest percentage of infectivity of the beet leafhopper in the San Joaquin Valley was obtained in 1932, when 66 per cent of the adults of the spring generation collected in the northern Hospital Canyon transmitted the curly-top virus to sugar beets, as compared with 31 and 42 per cent in Little Panoche Pass.

In 1933 a comparison was made of the percentages of infective adults of the spring generation collected in canyons—Hospital Canyon, Corral Hollow, and Lone Tree Canyon—situated in the northern San Joaquin Valley. The results are given in table 2.

During the spring, beet leafhoppers frequently congregate near the entrance of mountain passes (*16, 18*) and canyons before the flights into the cultivated areas occur. One hundred adults were collected on April 20, 1933, in an area of about 150 square feet of pasture vegetation near the entrance of Lone Tree Canyon, of which 12 per cent proved infective; and another 100 adults were captured in many localities in the same canyon, of which 15 per cent proved infective; the difference is probably not significant.

If the higher percentages of infective adults of the spring generation are associated with the assumption that the overwintering females reared on curly-top beets spread the virus to susceptible plants in the northern canyons, then it would be difficult to explain the lower percentages of infectivity obtained with the adults collected in Lone Tree Canyon, situated only a few miles away from Hospital Canyon. This discrepancy, however, forms a single exception to the general trend and should not be given too much emphasis. Beets were grown near Manteca and Union Island, situated 10 to 15 miles from the entrances of the three canyons.

On Foothills of the Salinas Valley—In the Salinas Valley, the favorable weeds in which the females deposit their eggs are not abundant, and the multiplication of the beet leafhopper occurs chiefly on beets; hence, higher percentages of infective overwintering leafhoppers should occur on the foothills of the Salinas Valley than on those of the San Joaquin Valley. Migrations of the spring-generation adults occur from the San Joaquin Valley to the foothills and cultivated areas of the Salinas Valley, as reported in a previous paper (*16*). The percentage of infectivity of the nymphs is more reliable than that of the adults during the spring in the Salinas Valley.

During 1925, 2,603 acres of beets had been grown near King City and 15,689 acres in the Salinas Valley, and a serious outbreak of sugar-beet curly top occurred that year. Sugar beets were grown near the base of the foothills east of San Ardo and on the Spreckels ranches near King City. The leafhoppers were commonly taken on *Erodium cicutarium* growing on the foothills west of San Ardo and near King City. A high percentage of infective overwintering adults and nymphs and adults of the spring generation occurred on the foothills, as shown in table 2.

During 1931, 278 acres of beets had been grown in the King City district and 1,304 acres in the Salinas Valley. As indicated in table 2, lower percentages of infective adults of the overwintering and spring generations occurred in 1932 in Pine Valley, situated between San Lucas and San Ardo.

During 1932, 1,050 acres of beets had been grown in the vicinity of King City and 8,508 acres in the Salinas Valley. The percentages of infective spring-brood adults collected in Hog Canyon near King City and on the foothills near Metz are given in table 2.

In Cultivated Areas.—After the 1925 outbreak of the beet leafhopper (*20*), overwintering adults were abundant in the beet fields of the Santa Clara and Salinas valleys. Planting of sugar beets was temporarily abandoned in these valleys during the season of 1925–26, owing to the fact that during the 1919 outbreak of the pest over one-half of the early

planted beets in the San Joaquin and Salinas valleys were infected with curly top by the overwintering females which remained in the cultivated areas (*10*).

Leafhoppers which remained in the cultivated areas during the winter were collected on February 23, 1926, in the beet fields from King City to Gonzales in the Salinas Valley, and 42 per cent were found to be infective. The insects probably invaded the beet fields from weeds growing in the cultivated areas: a large number of weeds (*17*) have been demonstrated to be naturally infected with curly top. A large flight of the adults of the spring generation occurred on April 19, and the next day 100 adults were collected on weeds growing in the cultivated areas near King City. Table 2 shows that 36 per cent of the leafhoppers were infective.

During 1932 the percentages of infective adults of the overwintering generation were higher than those of the spring generation in the Salinas Valley, as shown in table 2.

On Pasture Vegetation Germinating Early and Late.—The percentage of infectivity of the beet leafhopper may be associated with the time of germination of the seeds of the pasture vegetation by autumn or early-winter rainfall. When early-autumn rains germinate the seeds of host plants susceptible to curly top on the uncultivated plains and foothills at the time the flights occur from the cultivated areas, the opportunity for the spread of the disease is greater than during dry autumns or dry early winters, when the overwintering adults are forced to feed on perennial food plants, most of which are nonsusceptible to curly top. As more host plants become infected on the uncultivated plains and foothills, noninfective leafhoppers may pick up the virus and infective insects may become reinfected and thus their infective power may increase. The longer the insects are forced to feed on perennial noninfected food plants, the shorter the period of infectivity of the overwintering adults. It appears, then, if the infective power of the overwintering adults is reduced by feeding on perennial food plants, the spread of the disease to late-germinating pasture vegetation is limited, and hence a low percentage of infectivity of the adults of the spring generation should occur under natural conditions.

Many of the overwintering adults reared on curly-top beets in the northern San Joaquin Valley probably enter the northern canyons; and hence the percentages of infective beet leafhoppers in Little Panoche Pass, situated about 80 miles from the nearest beet fields, will be considered in relation to early and late germination of the seeds of the pasture vegetation. Most of the overwintering adults which fly into little

Panoche Pass breed on favorable weeds, such as Russian thistle (*Salsola kali* var. *tenuifolia*), bractscale (*Atriplex bracteosa*), and fogweed, or silverscale (*Atriplex argentea* subsp. *expansa*). As reported in a previous paper (*16*), migrations occur from the San Joaquin Valley to the foothills of the Salinas Valley, and hence the percentages of infectivity of the spring-generation adults in relation to early and late germination of the seeds of the pasture vegetation will not be discussed for the Salinas Valley.

TABLE 3

PRECIPITATION FOR THE AUTUMN AND EARLY WINTER, FIREBAUGH AND MERCY HOT SPRINGS

(In inches)

Day	Firebaugh								Mercy Hot Springs			
	1923			1925			1928,* Nov.	1929, Dec.	1930–31†		1931, Nov.	1932, Nov.
	Sep.	Oct.	Nov.	Oct.	Nov.	Dec.			Nov.	Jan.		
1	....	....	....	....	....	....	....	....	....	....	....	....
2	....	....	....	....	....	0.36	....	....	....	....	....	....
3	....	....	....	....	0.02	....	0.05	....	....	....	....	....
4	....	....	....	....	0.08	....	....	....	....	....	....	....
5	....	....	....	0.03	....	....	....	....	....	0.60	....	....
6	....	....	....	0.03	....	....	....	....	....	0.04	....	....
7	....	0.15	....	....	....	....	....	....	....	0.58	....	....
8	....	....	....	....	....	....	....	....	....	....	....	....
9	....	....	0.06	....	....	....	....	....	....	....	0.18	....
10	....	....	0.02	0.03	....	....	....	0.04	....	....	....	....
11	....	....	....	....	0.02	....	....	0.07	....	....	....	....
12	....	....	....	0.04	0.07	....	....	0.03	....	....	....	....
13	....	....	....	....	....	....	1.30	....	....	....	....	....
14	....	....	....	....	....	....	0.65	....	....	....	0.84	....
15	....	....	....	....	....	....	0.15	....	0.02	....	0.07	....
16	....	....	....	....	....	....	....	0.12	0.08	....	....	....
17	....	....	....	....	....	....	....	....	0.02	....	....	....
18	....	....	....	....	....	0.59	....	....	....	....	....	....
19	....	....	....	....	....	0.18	....	0.02	....	....	....	....
20	....	....	....	....	....	....	....	0.03	....	....	....	....
21	....	....	....	....	....	....	....	....	....	....	....	....
22	0.36	....	....	....	....	....	....	....	....	0.38	....	....
23	....	....	....	....	....	....	....	....	....	....	....	....
24	....	....	....	....	....	....	....	....	....	....	....	....
25	....	....	....	....	....	....	....	....	....	....	....	....
26	0.06	....	....	....	....	....	....	....	0.11	....	0.50	....
27	....	....	....	....	....	....	....	....	0.02	....	....	....
28	....	....	....	....	....	....	....	....	....	....	....	....
29	....	....	....	....	....	....	....	....	....	....	....	....
30	....	....	0.33	....	....	....	....	....	....	....	....	0.42
31	....	....	....	....	....	....	....	....	....	....	....	....
Total	0.42	0.15	0.41	0.13	0.19	1.13	2.15	0.31	0.25	1.60	1.59	0.42

* Rainfall for October, trace.

† Rainfall for December, 0.00.

The time of germination of pasture vegetation in Little Panoche Pass is of course related to the occurrence of the first rains. Table 3 shows the daily precipitation for the autumn and, in some years, for the early winter. No rainfall records are available during the years 1923, 1925, 1928, and 1929 at Mercy Hot Springs, situated in Little Panoche Pass, and hence the rainfall records at Firebaugh, situated in the valley floor about 25 miles from Mercy Hot Springs, are given.

During the first half of the autumn, about ½ inch of rainfall is sufficient to germinate the seeds of the pasture vegetation; during the last half of the autumn and early winter, when temperatures are lower and fogs are frequent, ¼ inch of rainfall is considered enough to germinate the seeds of the pasture vegetation. An examination of the daily precipitation (table 3) shows that for the years 1923, 1925, 1928, 1931, and 1932 there was sufficient rainfall for the seeds of the pasture vegetation to germinate during the autumn; and in Little Panoche Pass a high percentage of infective adults of the spring generation occurred (table 2). The rainfall records during 1929 and 1930–31 in table 3 show that there was not sufficient rainfall for the seeds of the pasture vegetation to germinate until winter; and in Little Panoche Pass the lowest percentages of infective adults of the spring generation occurred in these years (table 2).

There is one factor which may prevent the rapid autumnal spread of curly top to annual plants on the uncultivated plains and foothills. Young plants succumb much more rapidly to the disease than do older, deep-rooted plants. If the annual was young and infected with curly top by the overwintering female at the time of oviposition, the infected plant might die before the egg hatched, especially during the winter in the northern part of the San Joaquin Valley, when the egg period may require from 51 to 55 days (*15*). This of course diminishes the number of infective leafhoppers of the spring generation.

PERIOD OF INFECTIVITY DURING ADULT LIFE

Freitag (*4*) determined the period of infectivity during the adult life of the beet leafhopper, and the results are summarized in table 4. The outstanding result obtained with previously noninfective leafhoppers that fed for short periods on curly-top beets and were then transferred daily to healthy beets is the low percentages of infections obtained, as compared with those obtained from leafhoppers that fed for longer periods on diseased beets. Many of the infective leafhoppers apparently lost the capacity to produce infections during late adult life; others retained their infectivity but infected beets only at great intervals. The insect could be reinfected with the virus during late adult life; and it then

transmitted the virus as readily as recently molted adults. The evidence indicates that the curly-top virus does not multiply in the beet leafhopper and that the insects are merely internal mechanical carriers of the virus.

On Plants Immune to Curly Top.—Experiments were conducted to determine the ability of infective beet leafhoppers to transmit the curly-top virus after they had been transferred from diseased beets to immune

TABLE 4

SUMMARY OF RESULTS ON TRANSMISSION OF CURLY-TOP VIRUS BY SINGLE BEET LEAFHOPPERS FED FOR VARYING PERIODS ON A DISEASED BEET AND TRANSFERRED DAILY TO A HEALTHY BEET DURING ADULT LIFE*

Period on curly-top beets	Average number of beets inoculated	Beets infected		Average per cent of beets infected during					
		Average number	Average per cent	1–30 days	31–60 days	61–90 days	91–120 days	121–150 days	151–180 days
10, 20, 40, 60, 120, and 180 minutes..........	99.2	3.4	3.4	7.2	2.2	1.3	1.6	1.8	1.0
¼, ½, 1, 3, 7, 14, 21, and 28 days..........	130.7	15.1	11.6	26.5	15.0	5.6	3.9	0.5	0.0
Nymphal stages........	132.2	15.6	11.8	31.9	14.8	5.2	1.2	0.0	0.8
	138.6	16.6	12.0	28.3	12.9	11.4	1.2	4.1	4.1
	160.4	10.7	6.7	18.7	7.9	3.3	1.8	1.7	5.7

* Summarized from: Freitag J. H. Negative evidence on the multiplication of curly-top virus in beet leafhopper, *Eutettix tenellus*. Hilgardia **10**(9): 303–42. 1936.

breeding plants. Twenty large *Atriplex semibaccata* transplanted from the field were repeatedly inoculated by large numbers of infective leafhoppers, but all proved to be immune to curly top. Mammoth or Alameda sweet corn (*Zea Mays*) was also demonstrated to be immune to curly top (*21*).

Recently molted males which had completed the nymphal stages on diseased beets were transferred in lots of 50 to each *Atriplex semibaccata* and to each sweet corn plant. After the leafhoppers were kept on plants immune to curly top for a period of 30 days, 2 lots of 10 males were transferred singly to healthy sugar-beet seedlings for 1 day. The same procedure was repeated at the end of 60 days; but after 90 days, the number of insects was so reduced that 2 lots of 10 males were not always available. The results are indicated in table 5.

According to table 5, the average percentages of beets infected during successive 30-day periods by leafhoppers kept singly on beets for 1 day were as follows: *Atriplex semibaccata* 34.7, 14.1, and 6.7; sweet corn 27.3, 11.3, and 2.4. Corresponding figures obtained by Freitag (*4*) for sweet corn are as follows: 24.5, 6.8, and 3.1. There was a decrease in the percentages of beets infected during successive 30-day periods when the

insects were transferred singly from immune host plants and kept on beets for 1 day, which indicates that many of the infective leafhoppers lost the capacity to produce infection.

A comparison of the average percentages of beets infected during suc-

TABLE 5

TRANSMISSION OF CURLY-TOP VIRUS BY SINGLE INFECTIVE MALE BEET LEAFHOPPERS KEPT ON IMMUNE HOST PLANTS FOR PERIODS OF 30, 60, AND 90 DAYS AND ON HEALTHY BEETS FOR 1 DAY

Immune host plant	Beets infected of 10 inoculated		After 90 days on immune plants	
	After 30 days on immune plant	After 60 days on immune plant	Beets inoculated	Beets infected
Australian saltbush (fleshscale) (*Atriplex semibaccata*)				
No. 1	7	1	4	0
No. 2	4	0	4	0
No. 3	1	1	4	0
No. 4	3	2	2	0
No. 5	3	3	1	1
No. 6	4	1	0	..
No. 7	4	1	0	..
No. 8	6	2	0	..
No. 9	5	0	0	..
No. 10	5	2	0	..
No. 11	4	1	0	..
No. 12	4	2	0	..
No. 13	3	1	0	..
No. 14	3	2	0	..
No. 15	2	1	0	..
No. 16	1	2	0	..
No. 17	0	2	0	..
Total	59	24	15	1
Average per cent	*34.7*	*14.1*	..	*6.7*
Alameda or Mammoth sweet corn (*Zea Mays*)				
No. 1	4	2	8	0
No. 2	3	0	10	0
No. 3	3	0	9	0
No. 4	3	1	3	0
No. 5	3	0	3	0
No. 6	2	0	8	1
No. 7	5	2	0	..
No. 8	5	1	0	..
No. 9	4	2	0	..
No. 10	2	0	0	..
No. 11	2	1	0	..
No. 12	2	2	0	..
No. 13	1	3	0	..
No. 14	1	2	0	..
No. 15	1	1	0	..
Total	41	17	41	1
Average per cent	*27.3*	*11.3*	..	*2.4*

cessive 30-day periods as given in table 5, with the average percentages of infections during 1–30, 31–60, and 61–90 days obtained with leafhoppers which completed the nymphal stages on diseased beets as given in table 4 indicates that the juices from *Atriplex semibaccata* and sweet corn did not affect the period of infectivity of the beet leafhopper and probably had no effect on the curly-top virus.

When leafhoppers which completed the nymphal stages on diseased beets were provided with a healthy beet daily during adult life, or when infective adults were kept on immune plants, the highest percentages of infections were obtained during the first 30 days. The longer the overwintering adults are forced to feed on perennials nonsusceptible to curly top during dry autumns and dry early winters, the shorter is the period remaining for infectivity, and hence the spread of the disease by the overwintering adults to susceptible plants on the uncultivated plains and foothills would be reduced.

NATURAL HOST RANGE OF CURLY TOP AND FAVORABLE VIRUS RESERVOIRS

Annuals.—The natural host range of curly top and favorable virus reservoirs of the beet leafhopper in the cultivated areas and on the uncultivated plains and foothills have appeared in previous reports. Additional host plants are reported in this paper. Seventy-five species of plants in 48 genera belonging to 18 families have been reported in previous papers (*12, 13, 14, 17, 19, 22*) to be naturally infected with curly top. The annuals demonstrated to be naturally infected with curly top include 11 species of weeds on the uncultivated plains and foothills and 20 species of weeds or other wild plants in the cultivated areas (*17*). Seventeen species of annual economic plants and 11 species of annual ornamental plants were proved to be naturally infected with curly top, a total of 59 annuals.

Lessingia glandulifera (plate 2, *A*) and *Hemizonia virgata,* annual composits which serve as food plants of the beet leafhopper on the uncultivated plains and foothills, have been repeatedly tested but have not been found to be naturally infected with curly top. *L. glandulifera* transplanted from the field was not experimentally infected with curly top.

Biennials or Perennials.—After the return flights of the overwintering beet leafhoppers to the uncultivated plains and foothills during dry autumns, large numbers of leafhoppers congregate on perennials, most of which are not susceptible to curly top. Three perennials growing on the plains and foothills have been found to be naturally infected with curly top, but these are of minor importance as food plants of the adults

of the overwintering generation. The curly-top virus was repeatedly recovered from a naturally infected perennial—ballscale (*Atriplex fruticulosa*) (Chenopodiaceae)—during a period of six months, when the tests were discontinued. No similar tests were made with the other two species of naturally infected perennials—*Modiola caroliniana* (Malvaceae) and *Phacelia ramosissima* (Hydrophyllaceae).

The weeds and wild shrubs proved to be naturally infected with curly top in cultivated areas include 3 species that may be either annuals or biennials and 4 species of perennials. The virus was repeatedly recovered from one perennial—Mexican tea (*Chenopodium ambrosioides*) (Chenopodiaceae)—during a period of one year, after which no further tests were made. The perennial nightshade (*Solanum Douglassii*) (Solanaceae) was found to be naturally infected with curly top whenever a severe epidemic of the disease occurred; the virus apparently becomes more virulent at such a time and highly resistant weeds seem to become more susceptible to infection. The virus was recovered from 4 of 17 seedlings which were repeatedly inoculated by lots of 5 to 50 infective males. The virus was recovered from naturally infected perennial water smartweed (*Polygonium amphibium* var. *Hartwrightii*) and swamp smartweed (*P. Muhlenbergii*) (Polygonaceae), but no other tests were made with these weeds.

Among economic plants, potato (*Solanum tuberosum*) (Solanaceae), a herbaceous plant; Single or Plain parsley (*Petroselinum hortense*) (Umbelliferae), a biennial or short-lived perennial; and Hairy Peruvian alfalfa (*Medicago sativa*) (Leguminosae) and horse-radish (*Armoracia rusticana*) (Cruciferae), two perennials, were demonstrated to be naturally infected with curly top. The virus was rarely recovered from naturally infected horse-radish during the summer and not at all during the autumn, nor from cuttings grown from naturally infected horse-radish roots. No experiments have been conducted up to the present time to prove potato-tuber transmission of the virus or whether the virus could be recovered during the autumn and winter from parsley and alfalfa.

The ornamental flowering plants found to be naturally infected with curly top include 1 annual or short-lived perennial and 2 perennials. During the spring, the virus was transferred by previously noninfective beet leafhoppers from 6 of 7 naturally infected fish geraniums (*Pelargonium hortorum*) (Geraniaceae) to sugar beets, but during the autumn the virus was recovered from only 2 of the same plants. The perennial grass pink (*Dianthus plumarius*) (Caryophyllaceae) was demonstrated to be naturally infected with curly top, but no other tests were made.

Perennials Experimentally Infected.—Quailbrush, or lenscale (*Atriplex lentiformis*) (Chenopodiaceae), frequently grows 10 feet high and occurs on alkali flats and river benches. Six of 20 seedlings transplanted from the San Joaquin Valley were experimentally infected with curly top. In a previous experiment, 8 seedlings were experimentally infected with curly top, but one year later the virus was not recovered from the same plants. The 8 plants were then reinfected, and the virus was again transmitted by previously noninfective beet leafhoppers from only 2 of these to sugar beets.

Australian saltbush, or fleshscale (*Atriplex semibaccata*) (Chenopodiaceae), grown from seeds, showed a high degree of resistance to curly top; in fact, most seedlings were immune to the disease. Thirty seedlings were repeatedly inoculated with different lots of infective beet leafhoppers, but 27 of them could not be infected. The virus was not recovered a second time from 1 of 3 infected plants 23 days after the first recovery of the virus.

Atriplex semibaccata has not been found to be naturally infected with curly top. Some adults collected on *A. semibaccata* under natural conditions transmitted the curly-top virus to healthy sugar beets. On June 9, 1933, each of 50 adults of the spring generation captured on *A. semibaccata* growing on the foothills near Metz in the Salinas Valley was provided with a healthy beet seedling. It was found that 8 of 50 beets, or 16 per cent, developed typical symptoms of curly top. Some of the adults undoubtedly obtained the virus from other host plants of curly top growing on the foothills and, after the pasture vegetation became dry on the foothills, flew to *A. semibaccata* and retained the infective power.

In the Imperial, Salinas, and San Joaquin valleys, different lots of nymphs collected on large *Atriplex semibaccata* isolated from other breeding plants failed to transmit the curly-top virus to healthy sugar beets. On July 7, 1933, each of 50 nymphs collected on *A. semibaccata* growing on the foothills near Metz was provided with a healthy beet, but not a single case of curly top developed.

Nymphs bred on *Atriplex semibaccata* failed to obtain the curly-top virus even though infective adults were feeding on the same plants. In this experiment, 9 lots of 10 infective females oviposited for a period of 4 to 7 days in 9 large Australian saltbushes transplanted from the field. The females were then removed and played no further part in the experiment. Nine lots of 50 infective males which had completed the nymphal stages on diseased beets were confined in cages enclosing the saltbushes. Two hundred nymphs which hatched from eggs deposited in

the saltbushes were transferred in lots of 10 nymphs to 20 healthy beets, but not a single case of curly top developed.

Soap plant (*Chenopodium californicum*) (Chenopodiaceae) occurs in stream beds and on moist slopes of the foothills. The plants experimentally infected with curly top were grown from roots transplanted from the foothills of the Salinas Valley.

Alkali blite (*Suaeda moquini*) (Chenopodiaceae) grows commonly on

Fig. 1.—Spray equipment used to control the beet leafhopper on cattle spinach, or allscale (*Atriplex polycarpa*) growing in Tunney Gulch, San Joaquin Valley. This shrubby perennial saltbush is one of the most favorable food plants of the overwintering generation of beet leafhopper. It is green during dry autumns. (Courtesy, E. A. Schwing, Spreckels Sugar Company.)

alkali soil. The virus was recovered from 9 of 30 plants obtained in the San Joaquin Valley.

Tree tobacco (*Nicotiana glauca*) (Solanaceae), which was introduced from South America and occurs on the plains, in canyons, and in mountain passes of the San Joaquin Valley, was experimentally infected with curly top but has not been found to be naturally infected with the disease. The virus was recovered by previously noninfective beet leafhoppers from 6 of 10 experimentally infected seedlings and transferred to sugar beets. The overwintering leafhopper was rarely taken on *N. glauca* during dry autumns.

Perennials Nonsusceptible.—Two perennial saltbushes belonging to the family Chenopodiaceae serve as important food plants of the beet leafhopper during dry autumns. Large numbers of beet leafhoppers sometimes congregate on cattle spinach, or allscale (*Atriplex polycarpa*), a large perennial saltbush growing on the plains (fig. 1) in

mountain passes, and in canyons in the middle and southern San Joaquin Valley; but this shrub was not experimentally infected with curly top. Fifty-three small plants transplanted from the San Joaquin Valley were repeatedly inoculated by different lots of infective leafhopper, but the virus was not recovered by noninfective insects. In addition, 8 plants grown from seeds could not be experimentally infected with the disease.

Spinescale (*Atriplex spinifera*) (plate 1, *D*), another large perennial saltbush widely distributed on the uncultivated plains in the middle and southern San Joaquin Valley, also serves as a food plant of the leafhoppers during dry autumns, but 3 small plants transplanted from the field and 8 plants grown from seeds could not be experimentally infected with the disease.

Lepidospartum squamatum (Compositae) (plate 2, *B*, *C*) forms dense stands in the dry sandy stream beds of the Salinas River and its tributaries and in some of the mountain passes and canyons in the San Joaquin Valley. Owing to its wide distribution, it is one of the most important food plants of the beet leafhopper during dry autumns. Small plants removed from the field were not susceptible to curly top. All attempts to germinate the seeds were failures, hence the seedlings were not tested for experimental infection.

Gutierrezia californica (Compositae) (plate 1, *A*), a shrub from ¾ to ½ feet high, occurs on the uncultivated plains and foothills of the San Joaquin Valley. Overwintering adults are commonly taken on this plant before the seeds of the pasture vegetation germinate. Nine plants removed from the field were not susceptible to curly top.

Overwintering adults were commonly taken on *Haplopappus venetus* subsp. *vernonioides* (Compositae) (plate 2, *E*), a shrub from 1 to 2 feet high growing on the plains and foothills in the San Joaquin Valley. Twenty-six plants removed from the field and 21 plants grown from seeds were not susceptible to the disease.

Creek senecio (*Senecio Douglasii*) (Compositae) (plate 1, *B*), owing to its common occurrence, is a more important food plant of the overwintering beet leafhoppers in the Salinas than in the San Joaquin Valley. It is abundant in the Salinas River and tributaries and also occurs in dry stream beds, in canyons, and on the sandy or gravelly plains of the San Joaquin Valley. Twelve small plants removed from the field and 12 plants grown from seeds were not susceptible to curly top. The leaves were curled, and dark brown or black droplets of liquid (plate 2, *D*) exuded from the stems and leaves, but noninfective leafhoppers failed to recover the virus from the inoculated plants. Nymphs which hatched

from eggs deposited in *Senecio Douglasii* completed their life cycle in the greenhouse.

Alkali heath (*Frankenia grandifolia*) (Frankeniaceae) is common on the alkali plains and in canyons and mountain passes of the San Joaquin Valley and serves as a food plant of the overwintering beet leafhoppers during dry autumns. After the pasture vegetation becomes dry in the spring, males of the spring generation which do not fly into the cultivated areas were commonly taken on this plant. *F. grandifolia* on which beet leafhoppers were captured was not found to be naturally infected with curly top. The virus was not recovered by noninfective leafhoppers from plants on which repeated lots of infective insects had fed.

The overwintering beet leafhoppers were also taken on other perennials growing on the uncultivated plains and foothills during dry autumns, such as burro fat (*Isomeris arborea*) (Capparidaceae), buckbrush or chaparral (*Ceanothus cuneatus*) (Rhamnaceae), alkali mallow (*Sida hederacea*) (Malvaceae), common horehound (*Marrubium vulgare*) (Labatae), *Grindelia camporum* (Compositae), *Chrysopsis villosa* (Compositae), arrowweed (*Pluchea sericea*) (Compositae), and California sagebrush (*Artemisia californica*) (Compositae), but plants transplanted from the San Joaquin Valley were not susceptible to the disease. The overwintering adults have been taken on many other perennial species during dry autumns, but these have not been tested for natural and experimental infection with curly top.

RECOVERY OF CURLY-TOP VIRUS FROM IMPORTANT BREEDING PLANTS OF BEET LEAFHOPPER

During the past five years, attempts have been made to control the beet leafhopper, after the return flights from the cultivated areas to the uncultivated plains and foothills have occurred, by spraying perennials (fig. 1) on which leafhoppers congregate during dry autumns. The insecticide used consists of a mixture of 39 gallons of Diesel oil and 1 pound of pyrethrum extract. A second method of control of the beet leafhopper is by the destruction of the summer breeding plants near the foothills before the adults of the overwintering generation acquire the winged stage. One of the most important breeding plants, Russian thistle (*Salsola kali* var. *tenuifolia*), is destroyed by summer hoeing, dragging, or disking. The third method consists of burning Russian thistle during the autumn before the plants are torn loose and start rolling; this prevents the spread and reduces the seed supply. A more detailed report on the methods of control of the beet leafhopper has been published in a previous paper (*9*).

Although in the control program it was known that certain weeds are important breeding plants and also high populations of beet leafhoppers congregate on these weeds during the autumn flights, no information was at hand on the recovery of the virus from these infected weeds by single insects. Three species of annual saltbushes and Russian thistle serve as important breeding plants of the beet leafhopper in the cultivated areas. Bractscale (*Atriplex bracteosa*) is one of the most important breeding plants of the beet leafhopper, and high populations of the leafhopper of the summer and overwintering generations develop on this weed. Although large numbers of leafhoppers of the spring generation sometimes congregate on fogweed, or silverscale (*Atriplex argentea* subsp. *expansa*), and high populations of the summer generation develop, nevertheless this saltbush in most seasons is not as favorable for the development of large populations of the overwintering generation as *Atriplex bracteosa* and Russian thistle. Red orache, or redscale (*Atriplex rosea*), is a favorable host plant for the development of the leafhoppers of the summer generation but becomes dry too early for the development of the insects of the overwintering generation. Russian thistle is the most important breeding plant of the leafhopper, and high populations of the insects of the summer and overwintering generations occur on this weed.

Tests were made on recovering the curly-top virus with single previously noninfective males which were kept on the 4 species of infected weeds for periods of 2, 4, and 8 days, and also with single adults which completed the nymphal stages, requiring from 26 to 36 days in the greenhouse (*15*), on some of the same weeds. The 4 species of weeds were inoculated with the curly-top virus by 10 infective males for a period of 3 weeks or longer, and then the insects were removed from the weeds. Noninfective males, after feeding on each infected weed for periods of 2, 4, and 8 days, were transferred singly to healthy beet seedlings (table 6). The method usually adopted to obtain adults reared during the nymphal stages on infected weeds was to allow 10 infective females to oviposit in each species of weed for a period of only 4 days, so as to avoid high populations of nymphs, which drain the plants. To insure infection, 10 infective males were fed on the same weeds for 3 weeks and then were removed from the cages. After the nymphs which hatched from eggs deposited in each infected weed acquired the winged stage, each of 10 males was provided with a healthy beet (table 7).

Table 6 shows that single previously noninfective males which were kept on the 4 species of weeds for periods of 8 days produced higher average percentages of infections than single adults which fed on the infected weeds for 2 days. A comparison of the results obtained in tables 6 and

TABLE 6

INOCULATIONS OF HEALTHY BEET SEEDLINGS WITH CURLY-TOP VIRUS BY MEANS OF SINGLE PREVIOUSLY NONINFECTIVE BEET LEAFHOPPERS FED ON INFECTED WEEDS FOR PERIODS OF 2, 4, AND 8 DAYS

Infected weed on which insects fed	Insects on infected weeds, 2 days		Insects on infected weeds, 4 days		Insects on infected weeds, 8 days	
	Dates fed	Beets infected of 10 inoculated	Dates fed	Beets infected of 10 inoculated	Dates fed	Beets infected of 10 inoculated
Bractscale (*Atriplex bracteosa*)						
No. 1	Apr. 19–21	8	Apr. 19–23	10	Apr. 19–27	9
No. 2	Apr. 19–21	7	Apr. 19–23	7	Apr. 19–27	7
No. 3	Apr. 19–21	6	Apr. 19–23	9	Apr. 19–27	10
No. 4	Apr. 19–21	5	Apr. 19–23	9	Apr. 19–27	7
No. 5	Apr. 19–21	4	Apr. 19–23	9	Apr. 19–27	7
No. 6	Apr. 19–21	3	Apr. 19–23	5	Apr. 19–27	8
No. 7	May 7– 9	0	May 7–11	2	May 7–15	1
No. 8	June 5– 7	9	June 5– 9	8	June 5–13	9
No. 9	June 5– 7	8	June 5– 9	8	June 5–13	8
No. 10	June 5– 7	7	June 5– 9	7	June 5–13	9
No. 11	June 5– 7	7	June 5– 9	8	June 5–13	6
No. 12	June 5– 7	6	June 5– 9	7	June 5–13	10
Total	....	70	....	89	....	91
Average per cent	....	*58.3*	....	*74.2*	....	*75.8*
Fogweed (silverscale) (*Atriplex argentea* subsp. *expansa*)						
No. 1	Apr. 19–21	7	Apr. 19–23	10	Apr. 19–27	8
No. 2	Apr. 19–21	7	Apr. 19–23	10	Apr. 19–27	6
No. 3	Apr. 19–21	7	Apr. 19–23	8	Apr. 19–27	9
No. 4	Apr. 19–21	6	Apr. 19–23	8	Apr. 19–27	7
No. 5	Apr. 19–21	4	Apr. 19–23	9	Apr. 19–27	5
No. 6	Apr. 19–21	2	Apr. 19–23	7	Apr. 19–27	8
No. 7	May 7– 9	8	May 7–11	6	May 7–15	8
No. 8	May 7– 9	5	May 7–11	3	May 7–15	4
No. 9	May 7– 9	3	May 7–11	2	May 7–15	6
No. 10	May 7– 9	3	May 7–11	1	May 7–15	1
No. 11	May 7– 9	2	May 7–11	7	May 7–15	6
No. 12	May 7– 9	1	May 7–11	2	May 7–15	5
Total	....	55	....	73	....	73
Average per cent	....	*45.8*	....	*60.8*	....	*60.8*
Red orache (redscale) (*Atriplex rosea*)						
No. 1	Apr. 19–21	9	Apr. 19–21	8	Apr. 19–27	9
No. 2	Apr. 19–21	8	Apr. 19–21	9	Apr. 19–27	9
No. 3	Apr. 19–21	8	Apr. 19–21	8	Apr. 19–27	8
No. 4	Apr. 19–21	6	Apr. 19–21	8	Apr. 19–27	9
No. 5	Apr. 19–21	6	Apr. 19–21	8	Apr. 19–27	8
No. 6	May 7– 9	7	May 7–11	7	May 7–15	7
No. 7	May 7– 9	7	May 7–11	3	May 7–15	6
No. 8	May 7– 9	6	May 7–11	1	May 7–15	3
No. 9	May 7– 9	4	May 7–11	6	May 7–15	4
No. 10	May 7– 9	4	May 7–11	4	May 7–15	4
No. 11	May 7– 9	3	May 7–11	4	May 7–15	6
No. 12	June 5– 7	3	June 5– 9	4	June 5–13	3
Total	....	71	....	70	....	76
Average per cent	....	*59.2*	....	*58.3*	....	*63.8*

TABLE 6—(*Concluded*)

Infected weed on which insects fed	Insects on infected weeds, 2 days		Insects on infected weeds, 4 days		Insects on infected weeds, 8 days	
	Dates fed	Beets infected of 10 inoculated	Dates fed	Beets infected of 10 inoculated	Dates fed	Beets infected of 10 inoculated
Russian thistle (*Salsola kali* var. *tenuifolia*)						
No. 1	May 3–5	0	May 3–7	4	May 3–11	5
No. 2	May 5–7	2	May 5–9	1	May 5–13	8
No. 3	May 7–9	1	May 7–11	1	May 7–15	2
No. 4	June 5–7	7	June 5–9	5	June 5–13	8
No. 5	June 5–7	7	June 5–9	5	June 5–13	5
No. 6	June 5–7	6	June 5–9	5	June 5–13	5
No. 7	June 5–7	2	June 5–9	2	June 5–13	1
No. 8	June 5–7	1	June 5–9	2	June 5–13	9
No. 9	June 5–7	0	June 5–9	4	June 5–13	4
No. 10	June 28–30	0	June 28–July 2	1	June 28–July 6	1
No. 11	July 17–19	7	July 17–21	7	July 17–25	8
No. 12	July 17–19	5	July 17–21	2	July 17–25	3
No. 13	July 17–19	2	July 17–21	1	July 17–25	3
No. 14	July 17–19	1	July 17–21	2	July 17–25	1
No. 15	July 17–19	1	July 17–21	1	July 17–25	2
No. 16	July 17–19	1	July 71–21	0	July 17–25	5
No. 17	July 17–19	0	July 17–21	5	July 17–25	2
No. 18	July 17–19	0	July 17–21	3	July 17–25	3
Total	....	43	....	51	....	75
Average per cent	....	*23.9*	....	*28.3*	....	*41.7*

7 shows that single males which completed the nymphal stages on the 3 species of infected saltbushes produced the highest percentages of infections.

According to table 6, single previously noninfective males were not able to recover the virus often from some of the infected weeds, as illustrated by *Atriplex bracteosa* no. 7, *A. argentea* subsp. *expansa* no. 10, and many Russian thistles; also when the nymphal stages were completed on Russian thistle (table 7). It is evident that some Russian thistles are resistant to the curly-top virus, while from some plants the virus can be recovered very readily by single adults reared during the nymphal stages on them.

Previously noninfective males recovered the virus from the 3 species of saltbushes monthly during the season's duration of the weeds and transferred it to sugar beets. The insects recovered the virus after the stems became woody and yellow, with the older leaves dry but the younger ones still green.

Russian thistles grown from seeds have been experimentally infected with the curly-top virus, and the virus was also recovered from small

TABLE 7

Inoculations of Healthy Beet Seedlings with Curly-Top Virus by Means of Single Beet Leafhoppers which Completed the Nymphal Stages on Infected Weeds

Infected weed on which insects fed	Dates adults were transferred from infected weeds to beets	Beets infected of 10 inoculated
Bractscale (*Atriplex bracteosa*)		
No. 13	May 8	10
No. 14	May 8	8
No. 15	May 8	8
No. 16	May 8	6
No. 17	May 8	5
No. 18	May 8	5
No. 19	May 8	4
No. 1	June 1	7
No. 2	June 1	10
No. 3	June 1	9
No. 4	June 1	8
No. 5	June 1	10
No. 6	June 1	8
No. 20	July 11	10
No. 21	Sep. 29	8
No. 22	Oct. 1	10
No. 23	Oct. 4	8
No. 24	Oct. 10	9
Total	....	143
Average per cent	....	*79.4*
Fogweed (silverscale) (*Atriplex argentena* subsp. *expansa*)		
No. 1	June 1	8
No. 2	June 1	10
No. 3	June 1	7
No. 4	June 1	8
No. 5	June 1	8
No. 6	June 1	6
No. 13	July 19	10
No. 14	Sep. 29	10
Total	....	67
Average per cent	....	*83.7*
Red orache (redscale) (*Atriplex rosea*)		
No. 13	May 8	7
No. 14	May 8	5
No. 15	May 8	4
No. 16	May 8	3
No. 17	May 8	2
No. 18	July 20	10
No. 19	July 21	9
Red orache (redscale) (*Atriplex rosea*)—Continued		
No. 20	July 23	10
No. 21	July 23	10
No. 22	July 26	10
No. 23	Sep. 1	3
No. 24	Oct. 5	7
Total	....	80
Average per cent	....	*66.7*
Russian thistle (*Salsola kali* var. *tenuifolia*)		
No. 19	May 8	7
No. 20	May 8	5
No. 21	May 8	3
No. 22	May 17	10
No. 23	May 17	6
No. 24	May 17	4
No. 25	May 17	2
No. 26	May 17	2
No. 27	May 18	5
No. 28	May 22	5
No. 29	May 22	5
No. 30	May 22	4
No. 31	May 22	2
No. 32	May 22	2
No. 33	May 22	1
No. 34	May 31	10
No. 35	May 31	9
No. 36	May 31	7
No. 37	May 31	1
No. 38	May 31	1
No. 39	July 20	1
No. 40	July 27	2
No. 41	Aug. 7	3
No. 42	Aug. 7	3
No. 43	Aug. 7	2
No. 44	Aug. 7	1
No. 45	Aug. 8	5
No. 46	Aug. 8	1
No. 47	Sep. 23	1
No. 48	Oct. 5	6
Total	....	116
Average per cent	....	*38.7*

naturally infected plants during the 1919 outbreak of the beet leafhopper. During 1933, attempts were made to experimentally infect with the curly-top virus thrifty-growing Russian thistles (plate 3, *A*) with long internodes and linear leaves (plate 3, *B*) transplanted from sandy soil near Manteca on May 11, and stunted plants with short internodes, thick stems, and prickle-tipped leaves (plate 3, *C*) collected on the plains in the middle San Joaquin Valley. Thirteen plants were inoculated with the curly-top virus by lots of 10 to 20 infective leafhoppers for periods varying from 16 to 42 days. Repeated lots of 20 previously noninfective males were fed on the plants for 2 days and then each lot of insects was divided among 2 healthy beet seedlings. The virus was recovered from 5 of 8 thrifty-growing but not from 5 stunted plants.

The fact that Russian thistles with long internodes are more susceptible to curly top than stunted plants with short internodes is important because higher populations of beet leafhoppers usually occur on the former. In another experiment, a total of 69 Russian thistles were inoculated with the curly-top virus by infective leafhoppers during different seasons of the year; the virus was recovered by previously noninfective adults from 56 plants, while 13 plants, or 18.8 per cent, were resistant or immune.

Tests were made to determine the percentage of infective nymphs on Russian thistles under natural conditions. One hundred nymphs were collected on September 7, 1933 on large Russian thistles about 10 miles southwest of Modesto in the San Joaquin Valley, and 9 per cent transmitted the curly-top virus to sugar beets. Another test was made with 50 nymphs collected on the same date on Russian thistles isolated from other breeding plants near Nile Garden in the San Joaquin Valley, but not a single nymph transmitted the virus to sugar beets.

Bassia hyssopifolia is a favorable breeding plant of the summer generation of beet leafhopper. Fifty nymphs were collected on September 6, 1933, on tall plants near Gustine in the San Joaquin Valley, and each was provided with a healthy beet; but not a single case of curly top developed. Small plants removed from the field were found to be immune to curly top: 7 plants were each inoculated by lots of 10 infective males for periods varying from 18 to 28 days, but 7 lots of 20 noninfective males failed to recover and transfer the virus to 14 sugar beets. Fifty males and 80 nymphs bred on 2 plants inoculated by 10 infective females for periods varying from 38 to 54 days failed to recover the virus. It is evident that leafhoppers bred on plants immune to curly top are noninfective even though infective females were feeding on the plants during the egg and nymphal stages.

WEEDS WHICH ATTENUATE THE CURLY-TOP VIRUS

Carsner and Stahl (*3*) reported that by passage of the curly-top virus through sowbane, or nettleleaf goosefoot (*Chenopodium murale*) (plate 4, *A, B, C*) the virus was so attenuated that when transmitted to healthy

TABLE 8

INNOCULATIONS OF HEALTHY BEET SEEDLINGS WITH CURLY-TOP VIRUS BY MEANS OF SINGLE AND LOTS OF 10 BEET LEAFHOPPERS REARED ON WEEDS WHICH ATTENUATE THE VIRUS

Infected weeds on which insects fed	Dates adults were transferred from infected weeds to beets	Single-insect inoculations			Inoculation by lots of 10 insects		
		Beets inoculated	Beets infected		Beets inoculated	Beets infected	
			Number	Per cent		Number	Per cent
Sowbane (nettleleaf goosefoot) (*Chenopodium murale*)							
No. 1	June 4	30	1	3.3	0	..	....
No. 2	June 30	0	..	....	2	0	0.0
	Sep. 25*	10	0	0.0	10	1	10.0
No. 3	Aug. 2–3	10	3	30.0	8	5	62.5
No. 4	Aug. 29–Sep. 1	10	0	0.0	1	1	100.0
	Nov. 9–10*	10	3	30.0	2	0	0.0
No. 5	Aug. 29–Sep. 1	10	1	10.0	1	1	100.0
No. 6	Sep. 1–5	10	1	10.0	1	1	100.0
	Nov. 9–24*	10	2	20.0	4	4	100.0
No. 7	Sep. 25	10	1	10.0	10	0	0.0
No. 8	Sep. 25–Oct. 2	10	1	10.0	10	0	0.0
No. 9	Oct. 2	10	0	0.0	10	1	10.0
No. 10	Oct. 31–Nov. 13	10	1	10.0	6	3	50.0
No. 11	Nov. 1–15	10	0	0.0	10	4	40.0
No. 12	Nov. 6–Dec. 3	10	0	0.0	6	1	16.7
No. 13	Nov. 17–24	10	0	0.0	1	1	100.0
No. 14	Nov. 17–24	10	2	20.0	1	0	0.0
Total or *Average*		180	16	8.9	83	23	27.7
Lamb's-quarters (white pigweed) (*Chenopodium album*)							
No. 1	June 4–11	10	2	20.0	1	1	100.0
No. 2	June 4–11	10	1	10.0	3	3	100.0
No. 3	June 4–11	10	1	10.0	2	0	0.0
No. 4	June 4–21	10	1	10.0	1	1	100.0
No. 5	July 17–24	10	4	40.0	10	7	70.0
No. 6	Aug. 3	10	1	10.0	5	0	0.0
No. 7	Sep. 5	10	4	40.0	1	1	100.0
No. 8	Sep. 5–20	10	9	90.0	1	1	100.0
No. 9	Sep. 24	10	1	10.0	10	0	0.0
No. 10	Sep. 28	10	1	10.0	10	1	10.0
No. 11	Oct. 31	10	4	40.0	0	..	....
Total or *Average*		110	29	26.4	44	15	34.1

TABLE 8—(*Concluded*)

Infected weeds on which insects fed	Dates adults were transferred from infected weeds to beets	Single-insect inoculations			Inoculation by lots of 10 insects		
		Beets inoculated	Beets infected		Beets inoculated	Beets infected	
			Number	Per cent		Number	Per cent
Alkali blite (*Suaeda moquini*)							
No. 1	July 9	0	..	....	4	1	25.0
	Sep. 4–Oct. 11*	10	0	0.0	0	..	....
No. 2	July 9	0	..	....	1	1	100.0
No. 3	July 17–23	10	2	20.0	4	0	0.0
	Oct. 31*	5	0	0.0	0	..	....
No. 4	Aug. 4	10	2	20.0	2	0	0.0
	Aug. 9–Sep. 4	10	0	0.0	2	0	0.0
No. 5	Oct. 23	10	0	0.0	2	1	50.0
No. 6	Oct. 23	10	3	30.0	0	..	....
No. 7	Oct. 31	10	2	20.0	0	..	....
No. 8	Nov. 2	10	1	10.0	0	..	....
No. 9	Nov. 5	10	1	10.0	0	..	....
Total or *Average*		95	11	11.6	15	3	20.0
Curly dock (*Rumex crispus*)							
No. 1	Aug. 15	10	0	0.0	5	1	20.0
No. 2	Aug. 29–Sep. 5	10	0	0.0	1	1	100.0
No. 3	Aug. 29–Sep. 5	10	2	20.0	1	0	0.0
	Oct. 1*	0	..	....	5	4	80.0
No. 4	Aug. 29–Sep. 20	20	1	5.0	1	1	100.0
	Nov. 14–22*	10	0	0.0	4	2	50.0
No. 5	Sep. 5–29	10	0	0.0	1	0	0.0
	Oct. 31–Nov. 28	10	0	0.0	3	2	66.7
No. 6	Sep. 5	10	0	0.0	1	1	100.0
	Oct. 31–Nov. 3*	10	0	0.0	1	0	0.0
	Nov. 9–24*	0	..	....	8	1	12.5
No. 7	Oct. 2–5	10	3	30.0	9	1	11.1
No. 8	Oct. 2–5	10	2	20.0	4	4	100.0
No. 9	Oct. 5	10	1	10.0	10	1	10.0
No. 10	Oct. 5	10	1	10.0	0	..	....
No. 11	Oct. 5	10	0	0.0	1	1	100.0
No. 12	Oct. 5–10	10	2	20.0	3	3	100.0
No. 13	Oct. 6	10	5	50.0	3	2	66.7
No. 14	Oct. 9	10	0	0.0	5	4	80.0
No. 15	Oct. 9	10	2	20.0	7	7	100.0
No. 16	Oct. 9	10	4	40.0	2	2	100.0
No. 17	Oct. 9	10	3	30.0	5	4	80.0
No. 18	Oct. 10	10	1	10.0	2	0	0.0
Total or *Average*		220	27	12.3	82	42	51.2

* Second-brood adults.

young sugar beets it either failed to cause the disease or usually produced only mild cases.

Lackey (*7*) confirmed the previous work with *Chenopodium murale*. He reported that 2 leafhoppers with attenuated virus infected 8 of 22

beets inoculated, or 36 per cent; and 10 leafhoppers with attenuated virus infected 21 of 38 beets, or 55 per cent. Lackey (*8*) also found that lamb's-quarters, or white pigweed (*Chenopodium album*), attenuates the curly-top virus.

Carsner (*2*) found two perennials—alkali blite (*Suaeda moquini*) (plate 1, *C*) and curly dock (*Rumex crispus*)—that are resistant to the action of the curly-top virus and attenuate the virus when it is passed through them.

An experiment somewhat similar to the one performed by Lackey was conducted to determine the percentage of single adults and lots of 10 adults that could recover and transfer the virus to beets from the 4 species of experimentally infected weeds which attenuate the virus. Twenty-five infective female leafhoppers inoculated each weed with the curly-top virus and deposited eggs in each plant during a period of 10 days, and then the females were removed. Sometimes two broods of adults were reared on the same weed, the plant again being exposed to 25 infective females. The adults of each brood were transferred singly to 10 beets or in lots of 10 adults to 1 beet. The results obtained with weeds which attenuate the virus are indicated in table 8, but weeds from which the virus was not recovered are omitted.

A detailed comparison of the average percentages of beets infected cannot be made in table 8, since a larger number of beets were used with single insects than with lots of 10 insects. A compilation of the data shows that single insects tested with 10 beets did not transfer the virus so often as 10 adults on 1 beet.

A few points of interest may be summarized from table 8 as follows:

Chenopodium murale no. 2: Adults of the first brood produced no infections, while 10 lots of 10 insects of the second brood infected 1 of 10 beets.

Chenopodium murale no. 3: Single adults infected 3 of 10 beets and 5 lots of 10 insects infected 5 beets on August 2, but on August 3, 3 lots of 10 insects failed to produce infections.

Chenopodium murale nos. 7 and 8: Single adults infected 1 of 10 beets, but 10 lots of 10 leafhoppers failed to produce infections.

Chenopodium murale no. 9: Single adults failed to infect 10 beets while 10 lots of 10 insects infected 1 of 10 beets.

Adults reared on many of the weeds inoculated with the curly-top virus failed to recover the virus, which indicates that such weeds were highly resistant or immune. The virus was recovered from 14 of 34 *Chenopodium murale,* 11 of 15 *C. album,* 9 of 30 *Suaeda moquini,* and 19 of 37 *Rumex crispus* plants.

Chenopodium album was not a favorable breeding plant, and usually low populations of adults were reared, but on an occasional plant large numbers of adults were obtained. On 5 *C. album* plants, the nymphs failed to acquire the winged stage. *Suaeda moquini* was also an unfavorable weed to rear nymphs; the nymphal stages were prolonged and usually low populations of adults were obtained.

SUMMARY

Higher percentages of infective adults of the spring generation usually occurred in the northern canyons of the San Joaquin Valley than in Little Panoche Pass, situated in the middle San Joaquin Valley about 80 miles away from the nearest beet fields. In all probability many overwintering adults reared on curly-top beets flew into the northern canyons and spread the virus to susceptible plants, and hence higher percentages of infective adults of the spring generation resulted.

There appears to be a correlation between the percentages of infective beet leafhoppers of the spring generation and early or late germination of the seeds of the pasture vegetation by autumn or early-winter rainfall in Little Panoche Pass: for example, during five years when there was rainfall in November, the infectivity varied from 16 to 42 per cent; during two years with December or January rainfall, the infectivity varied from 2 to 6 per cent.

There was a decrease in the percentage of beets infected during successive 30-day periods by adults kept on plants immune to curly top and transferred singly to beets for 1 day. Many of the infective beet leafhoppers apparently lost the capacity to produce infection. The evidence indicates that the juices from the immune host plants did not affect the period of infectivity of the leafhoppers and probably had no effect on the curly-top virus.

With the additions reported in this paper, seventy-five species of plants in 48 genera belonging to 18 families, including 59 species of annuals, 1 annual or short-lived perennial, 3 biennials, 1 biennial or short-lived perennial, and 11 perennials, have been demonstrated to be naturally infected with curly top.

Three species of perennials growing on the uncultivated plains and foothills were found to be naturally infected with curly top, but 16 species of perennials which serve as food plants of the beet leafhopper during dry autumns and early winters were not susceptible to the disease. The longer the overwintering adults are forced to feed on perennials nonsusceptible to curly top during dry autumns and early winters on the uncultivated plains and foothills, the shorter is the period remain-

ing for infectivity; and hence the less the spread of the disease to susceptible annuals after their seeds germinate.

The virus was repeatedly recovered from ballscale (*Atriplex fruticulosa*) during a period of six months and from Mexican tea (*Chenopodium ambrosioides*) during a period of one year, after which no further tests were made.

Natural infection of the perennial nightshade (*Solanum Douglassii*) was found during severe epidemics of the disease and may be associated with increased virulence of the virus.

The curly-top virus was recovered from naturally infected fish geranium (*Pelargonium hortorum*) more often during the spring than during the autumn. This may be associated with a higher concentration of the virus during the spring.

Perennial seedlings, such as quailbrush, or lenscale (*Atriplex lentiformis*), and Australian saltbush, or fleshscale (*A. semibaccata*), showed a high degree of resistance to the disease. The virus was recovered from infected seedlings of *A. lentiformis,* but one year later the virus was not recovered from these same plants. When these plants were reinfected, the virus was recovered from 2 of 8 plants. Seedlings of *A. semibaccata* were rarely infected with curly top, and large old plants were immune. The virus was not recovered from 1 of 3 infected seedlings 23 days after the first recovery of the virus.

The recovery of the virus from weeds which serve as the most important breeding plants of the beet leafhopper obtained with single noninfective leafhoppers which fed on the infected weeds for periods of 2, 4, and 8 days, and with single adults which completed the nymphal stages on the infected weeds is given in tables 6 and 7. The most favorable virus reservoir was *Atriplex bracteosa,* followed by *A. argentea* subsp. *expansa,* then *A. rosea* and lastly Russian thistle. The virus was recovered from all infected plants of the 3 species of saltbushes, but 15 of 69, or 18.8 per cent, of the Russian thistles were immune.

The virus was recovered monthly by previously noninfective beet leafhoppers from the 3 species of infected saltbushes during the season's duration of the plants and transferred to beets.

The transmission of the curly-top virus by single and by lots of 10 adults reared on 4 species of infected weeds which attenuate the virus is shown in table 8. Adults reared on the 4 species of weeds inoculated with the curly-top virus frequently failed to recover the virus.

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Plate 1.—*A*, Branch of *Gutierrezia californica* showing linear leaves and disk flowers. This perennial shrub occurs on the uncultivated plains and foothills of the San Joaquin Valley, and overwintering adults are commonly taken on this plant during dry autumns. *B*, Branch of creek senecio (*Senecio Douglassii*) showing narrow lobed leaves and clusters of flowers. This perennial, owing to its common occurrence, is a more important food plant of the overwintering adults during dry autumns in the Salinas than in the San Joaquin Valley. (Compare with plate 2, *D*.) *C*, Branch of alkali blite (*Suaeda moquini*) showing cylindrical leaves. The curly-top virus is attenuated by passage through this plant. *D*, Branch of spinescale (*Atriplex spinifera*) showing spines bearing sessile leaves. This large perennial saltbush is widely distributed on the uncultivated plains and foothills in the middle and southern San Joaquin Valley and serves as a food plant of the adults of the overwintering generation during dry autumns.

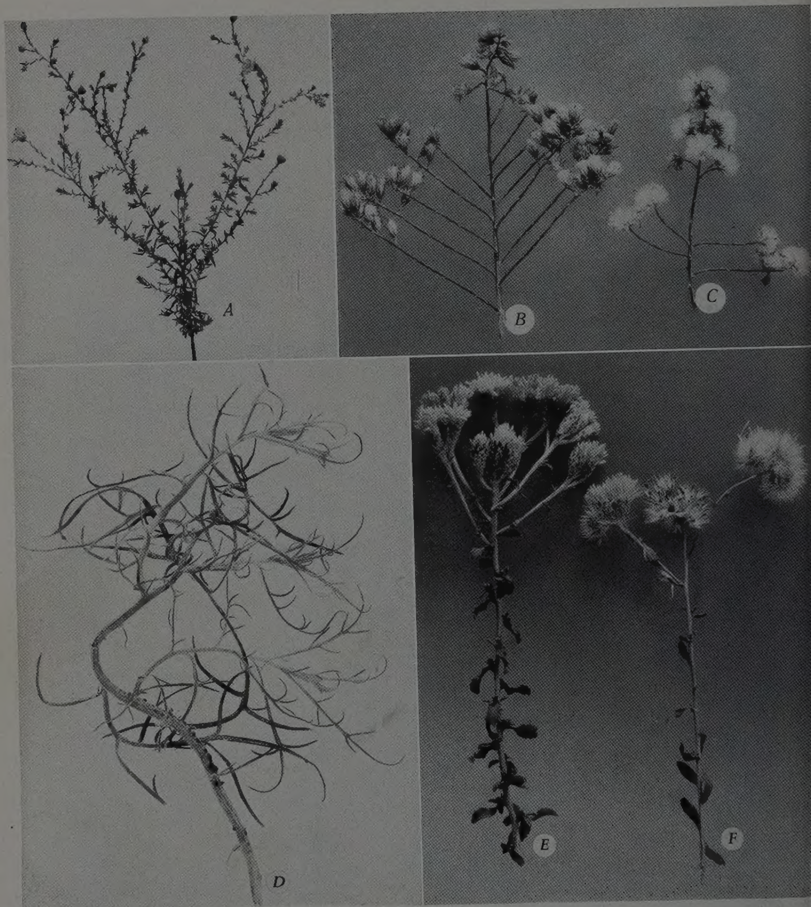

Plate 2.—*A*, *Lessingia glandulifera* showing erect branched stems bearing ovate or linear leaves and flowe This annual serves as a food plant of the overwintering adults on the uncultivated plains and foothills duri dry autumns. It has not been found to be naturally infected and was not experimentally infected with curly to *B* and *C*, *Lepidospartum squamatum*: *B*, branch showing flowers and scalelike leaves; *C*, branch showing brist arising from seeds. *D*, Branch of creek senecio (*Senecio Douglassii*) showing curled leaves and black dropl of liquid exuding from the stem; but noninfective leafhoppers failed to recover the virus from the inoculat plants. (Compare with plate 1, *B*.) *E* and *F*, *Haplopappus venetus* subsp. *vernonioides*: *E*, branch showi serrated, sessile leaves and clusters of flowers; *F*, branch showing silky pubescent arising from seeds. The ov wintering adults were commonly taken on this perennial shrub growing on the uncultivated plains and footh of the San Joaquin Valley during dry autumns.

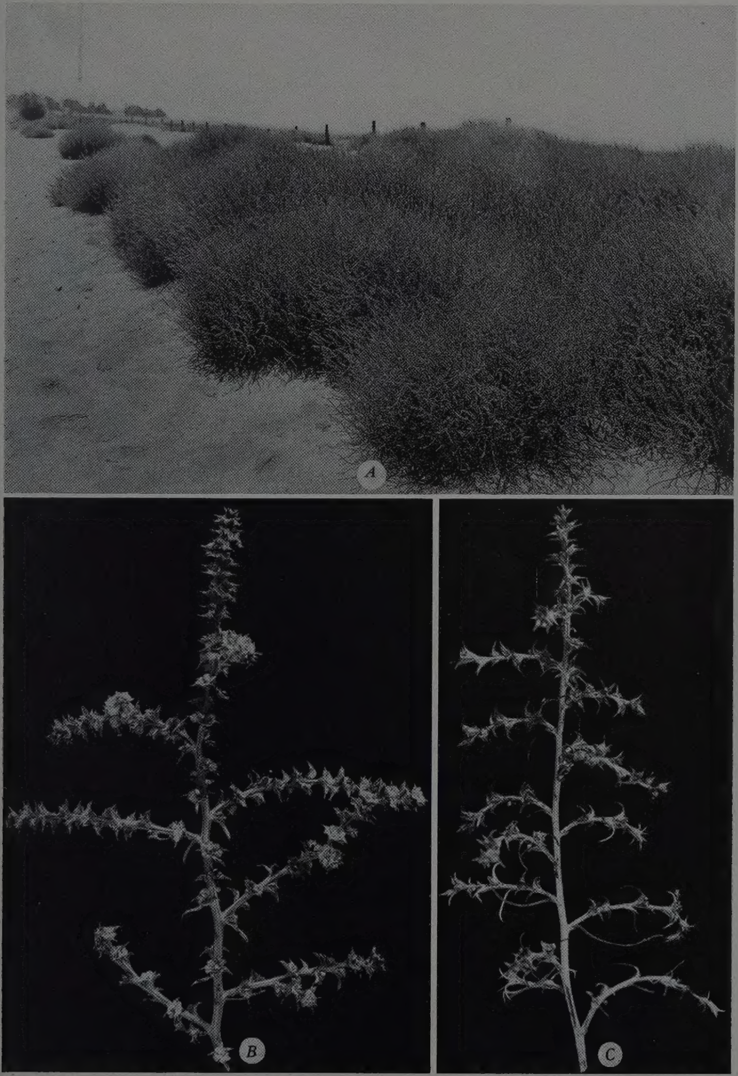

Plate 3.—Russian thistle (*Salsola kali* var. *tenuifolia*): *A*, plants growing in sandy soil along the roadside; *B*, branch from a large plant showing long internodes and linear leaves; *C*, branch from a stunted plant showing short internodes, thick stems, and prickle-tipped leaves. The leafhoppers multiply in enormous numbers on this plant in the interior regions of the state since it remains succulent from spring to autumn.

Plate 4.—Sowbane, or nettleleaf goosefoot (*Chenopodium murale*): *A*, secondary shoot from a plant experimentally infected with curly top showing curled apical leaves; *B*, branch and leaf from a healthy plant; *C*, plant experimentally infected with curly top showing secondary shoots with dwarfed leaves. The older leaves were removed from the middle portion of the plant. The virus is attenuated by passage through this weed and back to sugar beets.